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Site- and species-specific climatic responses of two co-occurring shrubs in the temperate Alxa Desert Plateau, northwest China

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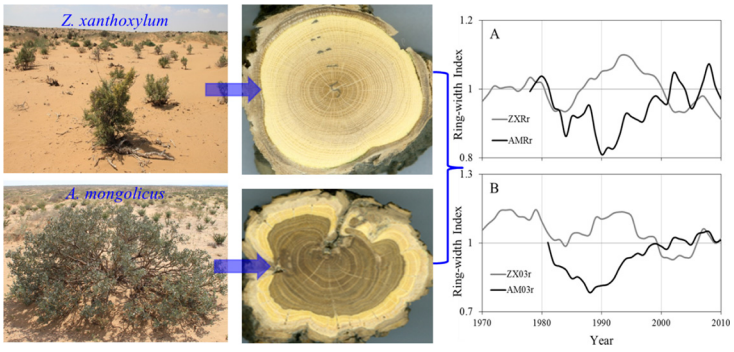
HIGHLIGHTS

- Radial growth of two co-occurring desert shrubs, *Z. xanthoxylum* and *A. mongolicus*, was mainly affected by precipitation.
- The climate response characteristics and changes between dry and wet periods exhibited spatial and temporal heterogeneity.
- Under climate change, the desert shrub populations will concentrated in better moisture micro-geomorphic regions.

GRAPHICAL ABSTRACT



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ABSTRACT

In the context of global precipitation anomalies and climate warming, the evolution of fragile desert ecosystems, which account for one-third of the world's land area, will become more complex. Studies of regional climate change and ecosystem response are important components of global climate change research, especially in arid desert regions. *Zygophyllum xanthoxylum* and *Ammopiptanthus mongolicus* are two dominant but endangered shrub species in the Alxa Desert in the arid region of central Asia. Using dendrochronological methods, we studied the response of radial growth of those two species to climate factors, and the adaptability of the two shrub populations under a regional warming trend. We found that radial growth of both shrubs was mainly affected by precipitation during the growing season. In additionally, along with the decrease of precipitation and the increase of temperature from east to west of Alxa desert Plateau, the limiting effect of drought during the growing season on radial growth increased. The climate response characteristics and changes between dry and wet periods exhibited spatial and temporal heterogeneity due to micro-level geomorphological factors. Under a regional climate warming trend, individual growth and population development of the two endangered shrubs will be adversely affected. In areas where these species are naturally distributed, populations will gradually become concentrated in micro-geomorphic regions with better soil moisture conditions, such as low-lying areas in the gullies that develop in alluvial fans. This finding has important scientific significance for understanding the development of the region's dominant shrub populations and protection of these and other endangered plants in arid desert areas.

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1. Introduction

The desert ecosystems in arid and semi-arid regions cover one-third of the global land area (Wei, 2000). In the context of global precipitation anomalies and climate warming, the evolution of fragile desert ecosystems will become more complicated. Studies of regional climate change and ecosystem response are important components of global climate change research, especially in arid desert regions (Wei, 2000). China's deserts are mainly distributed in the temperate and warm-temperate zones of western and northern China. Because these deserts are located far inland, they frequently experience drought due to small or infrequent rains. Desert plants, especially shrubs and dwarf shrubs, play an important role in maintaining ecological environment stability by preventing soil erosion and controlling desertification.

Tree rings provide a link between plant productivity and historical climate conditions. The analysis of shrub growth has therefore improved our understanding of vegetation dynamics in response to environmental changes. Shrubs provide a multi-decadal record of environmental and climate changes in treeless ecosystems (Lu and Liang, 2013), such as in deserts (Xiao et al., 2005, 2006, 2012, 2016; Oladi et al., 2017; Ding et al., 2018), arctic and alpine regions (Xiao et al., 2007; Liang and Eckstein, 2009; Liang et al., 2012; Myers-Smith et al., 2015).

Located within the zone of prevailing westerlies and on the northern fringe of the Asian summer monsoon region, vegetation in China's Alxa Plateau records the history of these different climate systems (Yang et al., 2003). The plateau is a representative sensitive ecological zone of western Inner Mongolia, northwestern China, and the central Asia desert region. The Helan Mountains in the east represent the western boundary of the East Asian summer monsoon, and also create a watershed between the internal and external flow areas of the region's deserts and the 200-mm rainfall isohyet. This desert plateau is also a major dust source for dust storms in central and eastern Asia (Wang et al., 2006).

There are many ancient Mediterranean, Quaternary, and regional endemic species in the area, such as *Haloxylon ammodendron*, *Zygophyllum xanthoxylon*, *Ammopiptanthus mongolicus*, *Tetraena mongolica*, and *Potaninia mongolica*, which reflect the complexity of the regional climate system and ancient paleogeographic changes. At the same time, climate change and human activities have gradually led to fragmentation of populations of some endangered or near-endangered species (Wang, 2005). Due to the long-term evolution of the vegetation in this harsh environment, key plant species are typically drought- and disease-resistant, and play a critical role in sand fixation and vegetation productivity (Chen, 2016). These species have therefore attracted the attention of plant physiologists, ecologists, and geographers for many years because they represent an ancient Tertiary flora relict with significant scientific value. Thus, it is urgently necessary to protect these species, particularly in the context of maintaining biodiversity throughout the arid region of northwestern China (Liu, 1998; Yuan et al., 2015).

In the Alxa desert Plateau, there are a few trees, so shrubs and dwarf shrubs are the optimum option for dendroecological research. Studies have shown that since 1988, the Alxa Desert has been characterized by a warming and drying trend (Xiao et al., 2017). Therefore, understanding the responses of radial growth of these species to climate change provides a good foundation for protection of the dominant shrub species and for understanding the mechanisms that underlie evolution of the deserts and regional desertification.

Vegetation in arid area is always limited by soil moisture, as the annual maximum NDVI significantly and positively correlate with the accumulated precipitation in the growing season (He, 2013). A remote sensing data based study in the Tengger Desert of the Alxa desert Plateau reveals that, the moisture condition is the key factor affecting the vegetation cover. Under the continued warming and drying trend during the period of 1999–2001, the vegetation coverage was reduced to its minimum during the period of 2000–2001 (Ma et al., 2006), and experienced little change from 2000 to 2012 (He, 2013). Micro-terrain is another important factor for the vegetation change. Li (2016) reported that the populations of *A. mongolicus* in mountainous areas and in areas with fixed and semi-fixed sands were decreasing, whereas the populations growing in alluvial fans were stable or increasing. Most of these studies were based on the whole ecosystem remote sensing data. As species-distinct response to climate change was found, more attention should be paid to the different species (Cuny et al., 2012).

The goals of this study were to examine the radial growth response of two co-dominant desert shrubs, *Z. xanthoxylum* and *A. mongolicus*, to short-term climate variations, to demonstrate that climate changes history are recorded by the growth rings of these species, and to evaluate their ability to survive the future regional warming. Under the background of climate warming and drying in the Alxa Desert, we hypothesized that (1) variations in the annual ring widths of the shrubs at two sites would be influenced by the regional climate change, and especially by precipitation before and during the growing season; (2) the response of shrubs to climate change, manifested in their radial growth, would be species- and site-specific; and (3) the climate change trend, characterized by warming, would influence the adaptability of two desert shrubs.

2. Materials and methods

2.1. Study area

The Alxa Desert is located on the north of the Hexi Corridor in China's Gansu Province and west of the Inner Mongolia Plateau (Fig. 1). The region lies between 37°N and 42°N and between 97°E and 106°E, and covers a total area of 27×10^4 km^2. The Alxa Plateau is an ancient high plain that has been extensively eroded. It contains three deserts: the Badain Jaran Desert, Tengger Desert, and the Ulanbuh Desert. Denuded mountains, gobis (desert with a gravel surface), and sandy desert are the main landscapes, and account for >70% of the total area.

The Alxa Desert has a typical continental climate with an average annual temperature ranging from 6.0 to 8.5 °C, with the lowest mean monthly temperature ranging from −7.5 to −11.1 °C in January and the highest mean monthly temperature ranging from 22.8 to 24.2 °C in July (Fig. 2). The precipitation decreases from the southeastern foothills (mean annual precipitation is about 210.2 ± 56.7 mm, the maximum was 348.4 mm in 1977 and the minimum was 112.2 mm in 1965) to the northwestern Gobi desert (mean annual precipitation is about 35.2 ± 19.5 mm, the maximum was 101.1 mm in 1969 and the minimum was 12.2 mm in 1972), and 70% falls from July to September. The measured annual evaporation increases from 2400 mm in the southeast to 4200 mm in the northwest. The climatic data were obtained from two meteorological stations, Zhongwei (37.53°N, 105.18°E, 1225.7 m a.s.l., 1960 to 2015) and Bayannuorigong (40.17°N, 104.80°E, 1323.9 m a.s.l., 1960 to 2015). The annual precipitation at these stations averaged 180 and 100 mm, respectively. The annual average temperatures were 9.0 and 7.4 °C, respectively. The underground water levels in the sampling sites are generally >4–6 m in depth and the fluctuation range is within 0.5–1.0 m around the year (Jiang et al., 2009; Zhang et al., 2015).

Z. xanthoxylum is a super-xerophilous plant that is endemic to central Asia's deserts. As a dominant and soil-stabilizing species, *Z. xanthoxylum* forms stable communities that are primarily distributed in desert and desert steppe areas (Xiao et al., 2012; Chen, 2016). *A. mongolicus* belongs to the Leguminosae family. It is an evergreen broad-leaved shrub that is unique to the deserts of central Asia. It belongs to a semi-exclusive (subspecial or nearly endemic) Chinese genus, and is now listed as a rare or endangered species. It is mainly distributed in the area from West Ordos to East Alxa. This species primarily occurs on sand dunes, gravel slopes, and terraces beside ravines with an arid climate. As a relict survivor of the evergreen broadleaf forest that existed in this region during the Tertiary period, *Ammopiptanthus* has a strong ability to adapt to dry and extremely cold environments (Shen et al., 2015).

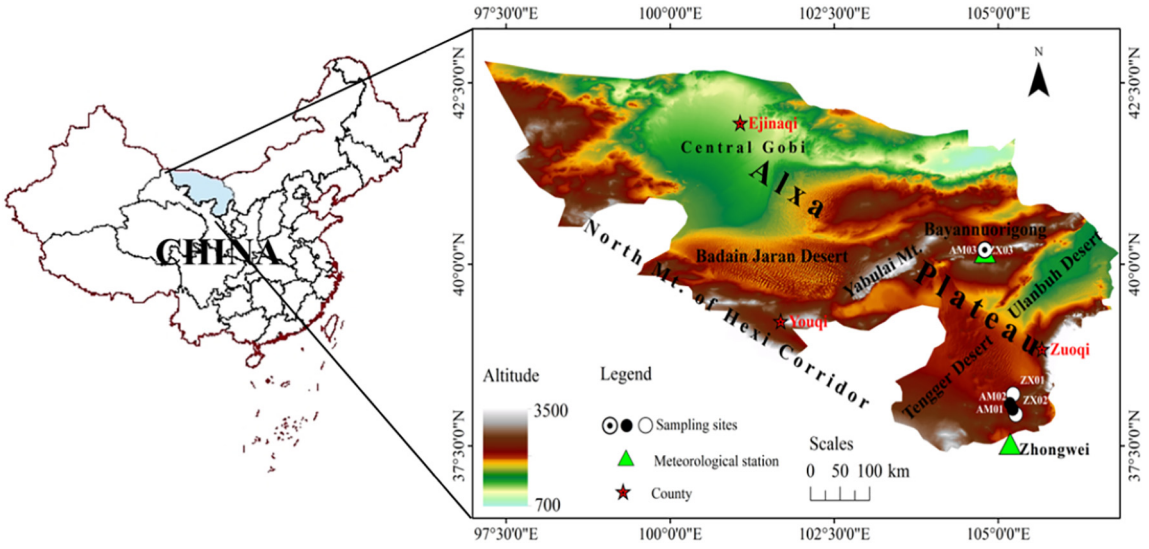

Fig. 1. Locations of the sampling sites and meteorological stations in the study area.

Both shrubs are dominant species in the region's gravel and sandy deserts and desertified grasslands, where they form communities that range from monocultures to complex vegetation assemblies. These communities play a critical role in sand fixation and vegetation productivity, which is important for maintaining the ecological balance of this arid desert region. At the same time, they have important scientific value for studying the occurrence and development of desert areas in northwestern China, its paleogeographic and paleoclimatic changes, and changes in its ancient flora (Wang, 2005; Zhou et al., 2015; Shi et al., 2018). Both species have been shown to have well-defined annual growth rings and suitable for tree-ring study (Xiao et al., 2012; Ding et al., 2018).

2.2. Field sampling and disc processing

We collected samples from six points (ZX01-ZX03 and AM01-AM03) in two sites, where those two species formed the dominant community. The eastern site was located at the border between the Helan Mountain alluvial fans and the Tengger Desert, and the central site was located in a low area of the Zongnai-Nuorigong Mountains (Fig. 1, Table 1). Both sites belong to desert steppe zone. The eastern site included two sample points of *Z. xanthoxylon* (ZX01 and ZX02), and two sample points of *A. mongolicus* (AM01 and AM02). The central site included one sample point of *Z. xanthoxylon* (ZX03), and one sample points of *A. mongolicus* (AM03).

At each sampling point, we selected 20 to 30 dominant shrubs with a stem diameter between 5 and 10 cm. We obtained one or two discs from each shrub. In the laboratory, all sample discs were dried, cut, sanded, and cross-dated. Before the measurements, we selected three to five intact discs with clear annual rings and a long chronology from among the sample discs at each site. We then measured the ring widths to an accuracy of 0.01 mm using the LINTAB measuring system (www.rinntech.de), with each disc measured in two randomly determined directions, producing 6 to 10 ring width curves at each site that we used as references for the remaining sample discs measurements. We discarded sample discs with extreme eccentricity or pith decay. Cross-dating and measurement quality control was carried out using the COFECHA software (Holmes, 1983).

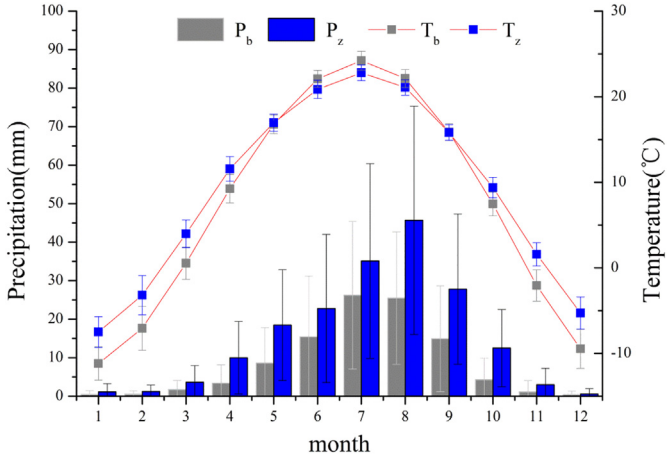

Fig. 2. Monthly average precipitation (P) and temperature (T) at the Bayannuorigong (P_b and T_b) and Zhongwei (P_z and T_z) meteorological stations.

2.3. Chronology assembly and data analysis

We used the ARSTAN software (Cook, 1985) to remove age-related growth trends and standardize the annual ring series. Depending on the variation of the ring width series, we used a negative exponential curve or a straight line to fit the growth trends at each site. We then processed the series of ring indices using the robust bi-weighted method to form a standardized index chronology. Generally, the subsample signal strength (SSS) index and the mean series intercorrelation (R_{BAR}) are used to evaluate the credibility and quality of the chronologies. The length of the trusted chronology is indicated by the parts of the series with a subsample signal strength (SSS) index >0.85. Another important statistic is the mean series intercorrelation (R_{BAR}), which is the mean correlation coefficient among the ring series and is therefore an indication of the common variance. The correlation between the chronologies of adjacent sampling sites was analyzed. Based on the correlation analysis results for each pair of ring width index series, we synthesized the final regional chronology using all the tree-ring width series at each site.

To reveal the main climate factors that limited radial growth of the shrubs, we used the DENDROCLIM2002 software (Biondi and Waikul, 2004) to analyze the correlation between the standardized ring-width chronology and the climatic factors (temperature and precipitation in each month and for certain ranges of months). The monthly mean temperature and monthly total precipitation from 1960 to 2015 were obtained from the China Meteorological Data Service Network (https://data.cma.cn/en) for the two nearest meteorological stations, in Zhongwei and Bayannuorigong (Fig. 1).

Table 1
Characteristics of the sampling sites.

Sampling sites	Geographic location and elevation	Habitat	Landscape
ZX01	38°12′34.2″N 105°13′34.8″E 1390 m	Sandy desert, wind erosion on the surface, the roots of Z. *xanthoxylon* are often exposed, and the plant height ranges from 1.0 to 1.5 m. Other species in the community include *Amygdalus mongolica* and *Nitraria tangutorum*.	
ZX02	37°55′59.1″N 105°16′03.6″E 1358 m	Sandy gravel desert, wind erosion on the surface, the roots of *Z. xanthoxylon* are often exposed, the growth is poor, the plant height is <0.6 m, and *Nitraria* nebkhas are well developed.	
ZX03 (AM03)	40°11′59.7″N 104°47′44.4″E 1307 m	Sandy gravel desert, with *A. mongolicus* mainly distributed in gulleys eroded by flooding in an alluvial plain; the growth is poor, and the plant height is 1.0 to 1.5 m. The *Z. xanthoxylon* is scattered in gobi areas, with a height < 0.5 m. *Reaumuria songarica* is an important species in the community, but other species include *N. tangutorum*, *Artemisia desertorum*, *Suaeda glauca*, *Potaninia mongolica*, and *Salsola passerina*.	
AM01	38°04′55.2″N 105°10′30.7″E 1334 m	Sandy desert, *A. mongolicus* is a dominant species in the community, with a height of about 1 m; other species include *Z. xanthoxylon*, *N. tangutorum*, and *Cynanchum hancockianum*.	
AM02	38°00′15.1″N 105°13′14.5″E 1335 m	Sandy desert, located in the Helan Mountains floodplain. Serious insect damage was observed on the leaves of *A. mongolicus*; the growth was poor, with height < 0.6 m, and other species include *Z. xanthoxylon* and *N. tangutorum*.	

3. Results

3.1. Statistical characteristics of the chronologies

The characteristics of the standardized ring-width chronologies for the six sampling points were summarized in Table 2. Compared to *Z. xanthoxylon*, the standardized chronologies of *A. mongolicus* were shorter. However, the standardized *A. mongolicus* chronologies had higher R_{BAR}, SD, MS, SNR, and PC1 values than the values for *Z. xanthoxylon*.

The correlation between the chronologies of adjacent sampling points was statistically significant (ZX01- ZX02: $F = 0.42$, $P < 0.01$; AM01-AM02: $F = 0.62$, $P < 0.01$). Therefore, we merged the data from the adjacent sampling points to construct new regional chronologies (ZXR and AMR, respectively) for subsequent analysis.

3.2. Comparison of the shrub's ring-width chronologies among sampling sites

Peak growth in the ZXR chronology appeared in 1934, 1943, 1975, and 2010. The smallest growth occurred in 1915, 1924 to 1930, 1950, 1951, 2006, and 2014 (Fig. 3A). In the ZX03 chronology, peak growth occurred in 1879, 1885, 1897, 1908, 1974, 1990, 1994, and 2012, and the smallest growth occurred in 1863, 1864, 1867, 1874, 1881, 1892, 1900, 1925, 1929, 1932, 1942, 1943, and 2014 (Fig. 3B).

Based on an analysis of the periodicity of the ZXR and ZX03 chronologies (data not shown), we smoothed the data using an 11-year moving window to reveal the low-frequency inter-decadal variation. The two chronologies (ZXRr and ZX03r) showed consistent trends and processes during their common periods (the gray bands in Fig. 3), with periods of relatively low growth from about 1915 to 1935, from the mid-1940s to the early 1970s, during the mid-1980s, and during the early 2000s. The other periods had relatively high growth.

The AMR regional chronology, which was constructed from the AM01 and AM02 chronologies, had peak growth in 1976, 1978, 1983, 1998, 2003, and 2007; the years with low growth were 1979, 1988, 2005, 2006, and 2008 (Fig. 4A). The peak growth recorded in the AM03 chronology occurred in 1998, 2007, and 2011; the years with low growth were 1987, 1988, 2006, and 2014 (Fig. 4B). As in the *Z. xanthoxylon* chronologies, we applied an 11-year moving-window

Table 2
Characteristics of the standardized ring-width chronologies.

	Sampling site					
	ZX01	ZX02	ZX03	AM01	AM02	AM03
No. directions/discs	56/31	53/27	39/26	70/36	32/22	54/27
Average length (yr)	60.3	61.5	84.9	19.7	24.5	23.4
Chronology length	1917–2015	1911–2015	1860–2015	1980–2015	1973–2015	1976–2015
SSS > 0.85	1934–2014	1953–2015	1920–2015	1999–2015	1995–2013	1998–2015
R_{BAR}	0.32	0.17	0.29	0.53	0.42	0.32
SD	0.19	0.20	0.18	0.20	0.32	0.22
MS	0.31	0.27	0.29	0.40	0.51	0.22
SNR	20.24	8.50	12.84	60.45	16.00	22.88
PC1	36.2	21.8	33.2	55.1	52.3	36.7

Abbreviations: MS, mean sensitivity; PC1, first principal component; R_{BAR}, mean series intercorrelation; SD, standard deviation; SNR, signal to noise ratio; SSS, subsample signal strength.

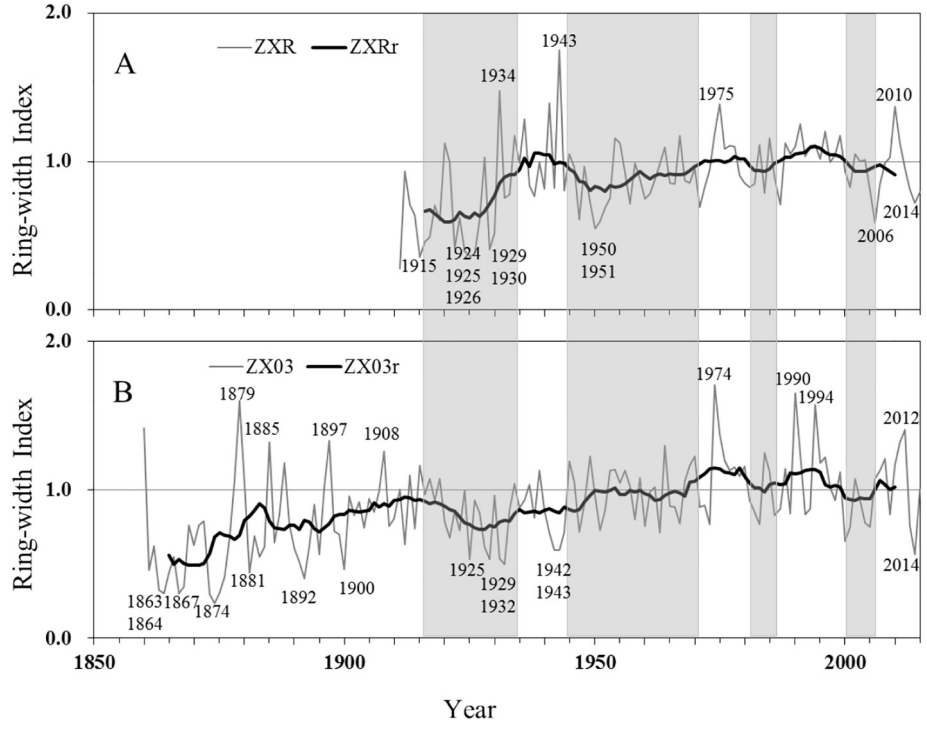

Fig. 3. (A) regional ring width standardized chronologies for *Z. xanthoxylon* (ZXR) and its 11-year moving-window smoothing (ZXRr); (B) local chronologies for the ZX03 site and its smoothed curve (ZX03r). The gray bands indicate the common period of low growth.

smoothing for the *A. mongolicus* chronology and found a common period of low growth from the early 1980s to the late 1990s (Fig. 4).

If we compare the smoothed curves for *Z. xanthoxylon* (ZXRr) and *A. mongolicus* (AMRr) in the eastern Alxa Desert (Fig. 5A), both chronologies recorded a growth decline and subsequent recovery from the late 1970s to the mid-1980s. Thereafter, *A. mongolicus* showed a dramatic growth decrease, reaching its lowest level in the early 1990s, while *Z. xanthoxylon* continued to recover and reached its peak growth in the mid-1990s. Afterwards, *Z. xanthoxylon* showed decreasing growth while *A. mongolicus* showed fluctuating growth recovery. In the 2000s, both species showed a more consistent trend of decreasing growth. Overall, the growth trends of the two shrubs from 1980 to 2000 were reversed. In the central Alxa Desert, *Z. xanthoxylon* (ZX03r) and *A. mongolicus* (AM03r) showed opposite

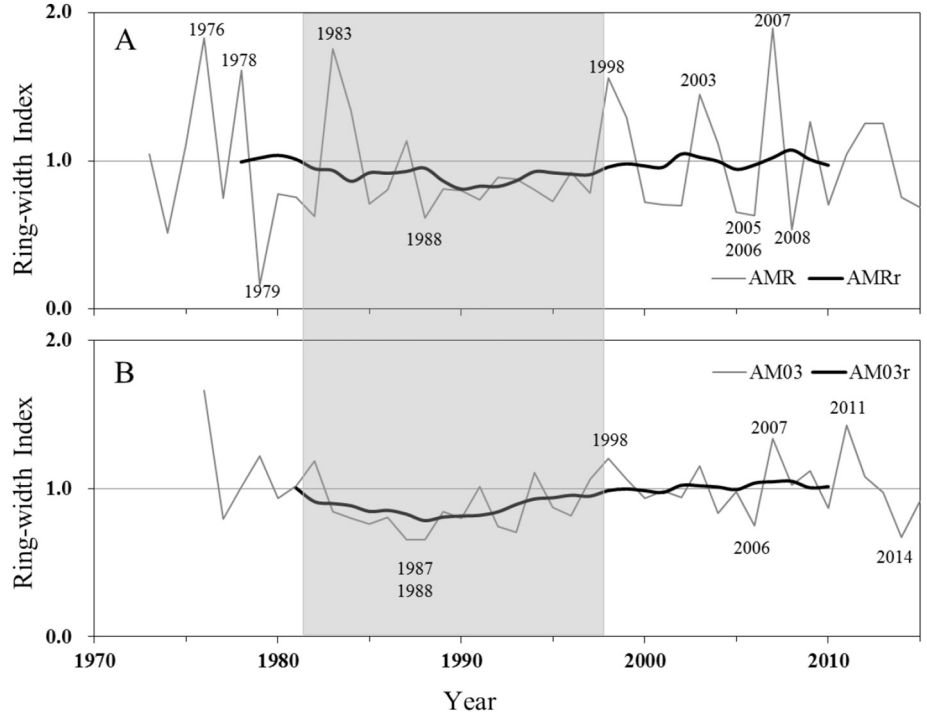

Fig. 4. (A) regional ring width standardized chronologies for *A. mongolicus* (AMR) and its 11-year moving-window smoothing (AMRr); (B) local chronologies for the AM03 site and its smoothed curve (AM03r). The gray band indicates the common period of low growth.

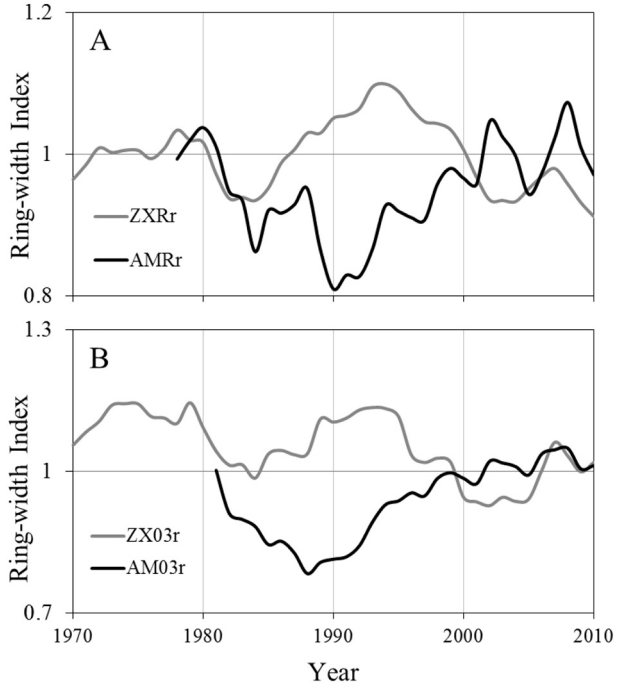

Fig. 5. Comparison of the smoothed (A) regional chronologies of *Z. xanthoxylon* (ZXRr) and *A. mongolicus* (AMRr) in the eastern Alxa Desert and (B) local chronologies of the two species (ZX03r and AM03r) in the central Alxa desert.

trends from the early 1980s to about 2005, with more consistent growth thereafter (Fig. 5B).

3.3. Relationships between the standardized ring-width chronologies and climatic factors

We found that the ZXR chronology significantly negatively correlate with the monthly mean temperature in May of the current year (Fig. 6). We observed a significant positive correlation between the ZXR chronology and monthly mean precipitation in the previous November, the current May, and the sum precipitation from October to December of the previous year and March to May of the current year. We found a similar pattern for the ZX03 chronology, but the chronology significantly negatively correlate with the mean monthly temperature in the current February, March, and July and the mean temperature from March to June, but significantly positively correlated with monthly mean precipitation from October to December of the previous year and from May to June of the current year.

The AMR chronology was significantly positively correlated with the monthly mean temperature in October of the previous year (Fig. 7), and significantly positively correlated with the monthly mean precipitation in May and June of the current year (Fig. 7), and in the May–July period. The AMR03 chronology showed a broadly similar pattern, but the significant correlations were found with the February and June temperature in the current year.

In general, the radial growth of *Z. xanthoxylon* and *A. mongolicus* in the eastern Alxa Desert was mainly affected by the precipitation in the previous winter (from October to December) and current growing season (from March to July). But for species in the central Alxa Desert, the radial growth of *Z. xanthoxylon* was inhibited by the high temperature.

4. Discussion

4.1. Growth response to climate

The soil moisture is the major limiting factor of *Z. xanthoxylon* radial growth (Fig. 6), supporting our first hypothesis, as indicated by the significantly positively correlation with growing season precipitation and negatively correlation with growing season temperature. This is the same with the previous research on *Z. xanthoxylon* in the Badain Jaran Desert, in the central Alxa Plateau, which also found a positive correlation between *Z. xanthoxylon* growth and precipitation during the current and previous growing seasons (Xiao et al., 2012). As a shrub species in arid area, 75% of the roots of *Z. xanthoxylon* were concentrated within the top 40 cm of the soil, and the major stem and leaves growth period was from April to June, when both precipitation and temperature were suitable (Zhou et al., 2006). As the local groundwater depth was nearly 4–6 m with slight fluctuation, the species mainly relies on the absorption of shallow soil water, which mainly comes from precipitation (Chen, 2016).

A. mongolicus, which is the only evergreen shrub species in the Asian desert region, has a strong main root, but it does not penetrate the soil deeply (to a depth of about 80 cm). This species has numerous lateral roots, producing a root biomass that can be >4 times the aboveground biomass, but 82% of the roots are distributed within the top 30 cm of the soil (Sun and Yu, 1994). Isotope-based hydrological research has shown that the water content of *A. mongolicus* mainly comes from precipitation (Chen, 2016). Large-scale phytogeography research showed

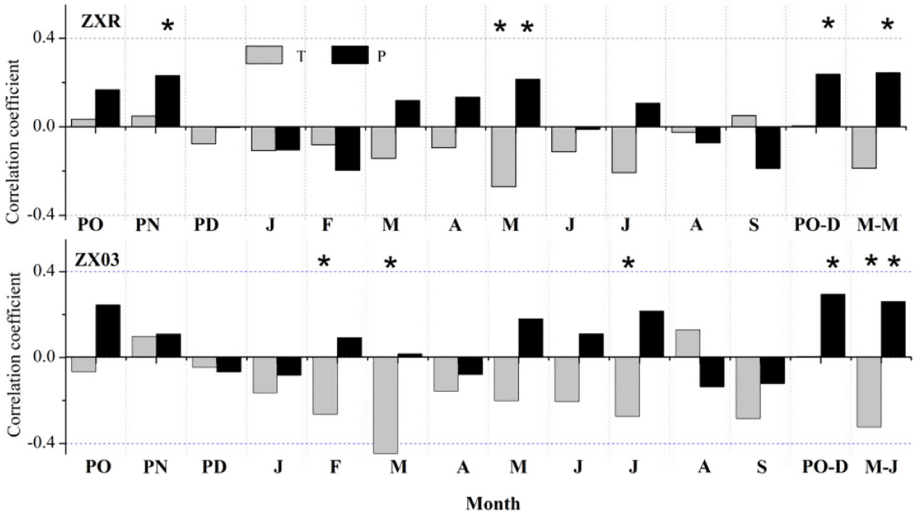

Fig. 6. Climate response characteristics of the *Z. xanthoxylon* chronology. PO to PD refer to October to December of the previous year. M-M and M-J refer to the periods from March to May and May to July in the current year, respectively. T: Temperature; P: Precipitation; Bars labeled with an * indicate a statistically significant correlation ($P < 0.05$).

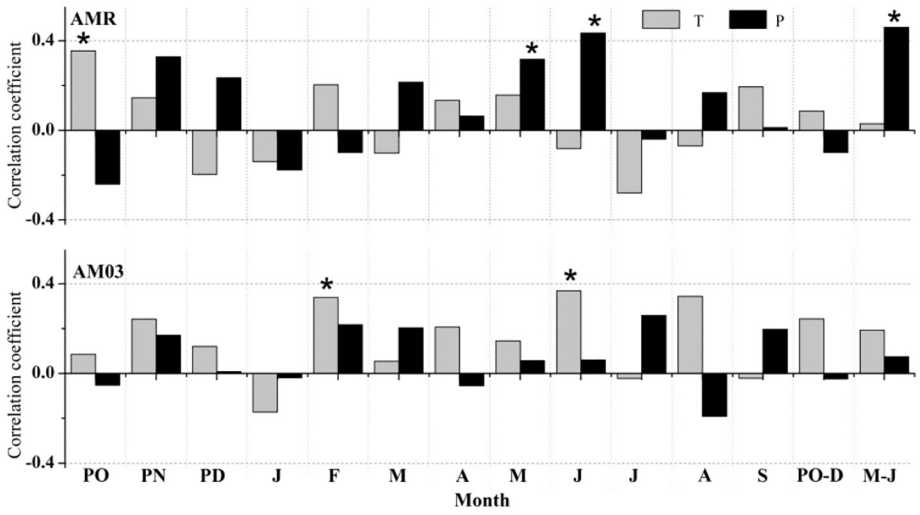

Fig. 7. Climate response characteristics of the *A. mongolicus* chronology. See Fig. 6 for abbreviations and stars.

that soil moisture factors are the main factors that limit the geographical distribution of *A. mongolicus* (Liu et al., 2017).

In the present study, we found inconsistent climate responses between the AMR and AM03 chronologies of *A. mongolicus*. The AMR chronology mostly positively correlated with the precipitation during the growing season, including the monthly mean precipitation in May and June and the total precipitation from May to July in the current year, and significantly positively correlated with the previous October's temperature (Fig. 7). In contrast, the AM03 chronology showed significant positive correlations with temperatures in February and June. For AM03, the sampling site was located at low to moderate elevations in an alluvial floodplain in the center of the Alxa Desert. The precipitation during the growing season was 40 to 75 mm, and combined with a warmer temperature (by nearly 2 °C), this creates more severe climatic conditions than in the eastern region, where the precipitation is 118.4 mm from April to July. So that, the limitation effects of the temperature in the growing season was stronger in the central Alxa Desert than in the eastern areas (Fig. 6).

Our sample of *A. mongolicus* was mainly distributed along a gully eroded by flooding (with a depth of 10 to 50 cm, and a width of 5 to 10 m; Table 1), indicating that the precipitation in this area cannot meet the needs of *A. mongolicus* on the gravel Gobi surface. In contrast, by growing in gullies below the surface, *A. mongolicus* may obtain access to deeper water that it cannot reach when it grows on the Gobi surface. The *A. mongolicus* plants are present as non-zonal vegetation and as a non-dominant species in this region, and were only found in microhabitats with better soil moisture conditions. The bio-zonal theory of vegetation distribution patterns suggests that the 120-mm rainfall isohyet defines the boundary between grassland vegetation and desert vegetation. The 70-mm rainfall isohyet represents the boundary between sparse dwarf shrubs and low-lying catchment area agglomerations of vegetation with <10% vegetation cover (Legendre and Fortin, 1989; Crawford, 2000). This is because low-lying areas such as erosion gullies can harvest and store runoff, which improves water availability to *A. mongolicus*. This may explain why the positive correlation between the AM03 chronology and precipitation during the growing season was not significant (Fig. 7). Therefore, we hypothesize that the redistribution of precipitation by the micro-scale geomorphology leads to different responses of radial growth to the climatic factors between *A. mongolicus* and *Z. xanthoxylon* in same region, as well as to the differences compared with plants in the eastern region. A previous survey of *A. mongolicus* communities growing in association with different landform types showed that the populations in mountainous areas and in areas with fixed and semi-fixed sands were decreasing, whereas the populations growing in alluvial fans was stable or increasing (Li, 2016). This agrees with our hypothesis that the water environment is crucial for this species.

A simulation and evaluation of the potential distribution of *A. mongolicus* using a population distribution model indicated that the most suitable area was located in the Helan Mountains floodplain in the eastern Alxa Desert, with a second suitable area in the Tengger Desert (Ma et al., 2012). The precipitation in these areas ranges from 100 to 200 mm, which suggests better water availability than at our study sites. At the same time, climate was the dominant limitation on the potential distribution of *A. mongolicus*, with precipitation pre- and during the growing season being important (Ma et al., 2012).

In research on the physiology and genetics of plant resistance to drought and cold, *A. mongolicus* has been used as a model plant. In a comparison with the genes reported from other plants, 528 (33%) of the Z. xanthoxylon genes found in the Unigene database were identified as stress-responsive genes (Liu et al., 2013). The leaves of *A. mongolicus* can withstand temperatures as high as 65 °C, and can survive temperatures as low as −30 °C. Even the seedlings can endure temperatures as low as −20.9 °C (Liu and Qiu, 1995). This leads us to believe that the positive correlation between the *A. mongolicus* chronology and the growing season temperature may be a statistically false correlation. The water conditions appear to be the most important climatic factor that affects the distribution and growth of this species.

Similarly, the dendroclimatiological studies in the surrounding mountains of Alxa desert Plateau, such as Helan, Changling-Shoulu and Dongdashan Montains, showed that the radial growth of two alpine trees, Qinghai spruce (*Picea crassifolia*) and Chinese pine (*Pinus tabuliformis*), are all controlled by the precipitation and high temperature in the growing season (from March to August) (Liu et al., 2004; Shi et al., 2005; Chen et al., 2012; Liu et al., 2013; Zhao et al., 2013). These studies all showed that the soil moisture condition is the main limited environment factor to the forest growth, whether the alpine trees or desert shrubs in the arid regions in north China.

4.2. Adaptability of the two shrubs to increasing temperatures

Meteorological observations showed that the temperature during growing season (from March to August), the temperature at both stations has increased by 0.25 to 0.29 °C per decade since 1960, in the eastern sit, the mean annual temperature(T_z) has risen by 1.2 °C since 1998. There was no significant change in precipitation during the growing season. The annual precipitation in the eastern (P_z) and central (P_b) regions showed high variation, with values (mean ± SD) of 131.7 ± 47.2 mm and 79.3 ± 34.5 mm, respectively, from 1960 to 2015 (Fig. 8). This

may explain why the three chronologies for *Z. xanthoxylon* present a clear trend of decreasing radial growth since the 1990s (Fig. 8).

Based on the climatic responses of radial growth of *Z. xanthoxylon* and *A. mongolicus*, we found that precipitation during the growing season is the main factor that limited the growth of the two shrub species. The limiting effect of temperature during the growing season on radial growth also increased from the eastern region to the central region (Figs. 6, 7). Increased temperature during the growing season will increase evapotranspiration of both shrub species, which will eventually lead to soil water deficits given the arid growing conditions, thereby reducing shrub growth, especially for *Z. xanthoxylon*, which is sensitive to both precipitation and temperature, and for *A. mongolicus* in the eastern region. For *A. mongolicus* in the central margin of the gobi, the shrubs appear to be at the edges of their natural distribution area, but the confluence of runoff from the mountains has greatly increased the water supply, which can reduce the impact of increased water consumption due to warming. A simulation of the potential distribution of *A. mongolicus* using a population distribution model indicated that the most suitable area for *A. mongolicus* was located in the Helan Mountains floodplain in the eastern Alxa Desert (Ma et al., 2012).

Higher seed germination rates for *A. mongolicus* and the longer radicle of *Z. xanthoxylon* seedlings suggest different adaptation strategies for the two shrubs (Shen et al., 2015). The radicle length of *A. mongolicus* (<2.3 cm) is shorter than that of *Z. xanthoxylon* (<14.6 cm), indicating a lower ability of seedlings to reach subsurface water and resist water stress. Stepwise regression analysis showed that salinity was the dominant factor that influenced seed germination and seedling growth, followed by drought, under a combination of salinity and drought stress (Shen et al., 2015). Under the significantly rising trend of regional temperatures, increased evaporation from the soil will increase salinization of the soil, and will eventually decrease seed germination. In our study area, drought is often accompanied by the outbreak of pests that take advantage of the weakened plants, especially for *A. mongolicus*, with hundreds of insects observed feeding on its flowers, pods, seeds, leaves, and roots from March to October (Wang, 2005). Insect damage can decrease plant growth, seed set, and the germination rate, as well as the development of individual plants and the evolution of populations.

Zygophyllum xanthoxylon has a main stem that is 10 to 20 cm long, and then forms secondary branches. In contrast, *A. mongolicus* has no obvious main stem, and many branches emerge from the rhizome at a steep angle from the vertical, and can form a large shrub. Therefore, *Z. xanthoxylon* is often subject to wind erosion, resulting in exposure of its near-surface roots, thereby decreasing its growth. By contrast, the dense branches of *A. mongolicus* offer stronger resistance to the wind, often leading to the formation of vegetated dunes that decrease evaporation of the shallow soil moisture, thereby improving the soil moisture supply to some extent.

In general, *Z. xanthoxylon* and *A. mongolicus* are the dominant shrubs in the Alxa Desert. However, under the global and regional warming trends, the available water will become increasingly inadequate, leading to declining growth and growth fluctuation in response to interannual variations of rainfall, especially in areas with fixed and semi-fixed sands. The *A. mongolicus* communities established in gullies in alluvial fans will be less strongly affected because the gullies tend to capture water. However, the populations of both species will gradually become concentrated in areas with micro-geomorphic conditions that improve water availability, such as low-lying areas of alluvial fans.

5. Conclusions

We found that both shrubs were most strongly affected by precipitation during the growing season. The climatic responses of the *Z. xanthoxylon* ring-width chronologies were consistent in the eastern and central regions of the Alxa desert. However, due to the influence of the micro-geomorphology of its preferred habitat, *A. mongolicus* in the central region responded weakly to precipitation. Under the observed regional climate change trend, which is characterized by strong warming, the growth of individual plants and the development of communities of these endangered shrubs will be adversely affected. Soil moisture stress will lead to disappearance of the shrubs in many areas, leading to concentration of the communities in areas with ample soil moisture conditions.

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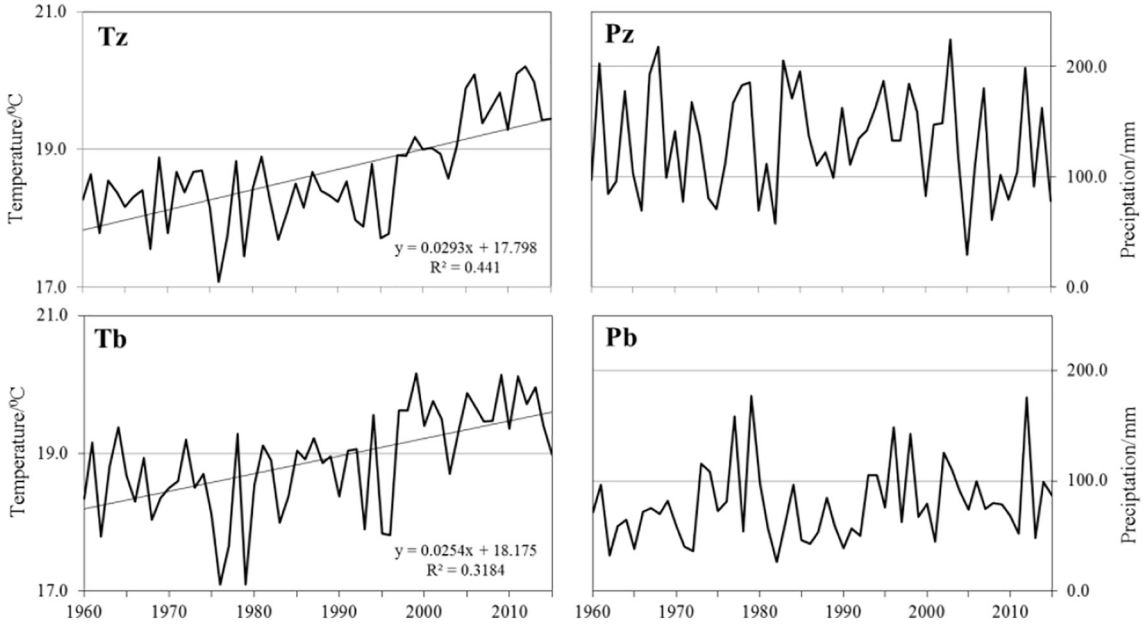

Fig. 8. Precipitation (P) and temperatures (T) during the growing season (from March to August) in the study area. (T_z and T_b represent temperatures and P_z and P_b represent precipitation at the Zhongwei (z) and Bayannuorigong (b) weather stations, respectively. The lines in the T_z and T_b graphs represent statistically significant trends.

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